

## A new look at age and area: the geographic and environmental expansion of genera during the Ordovician Radiation

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**Abstract.**—Although available paleobiological data indicate that the geographic ranges of marine species are maintained throughout their entire observable durations, other evidence suggests, by contrast, that the ranges of higher taxa expand as they age, perhaps in association with increased species richness. Here, I utilize a database of Ordovician genus occurrences collected from the literature for several paleocontinents to demonstrate that a significant aging of the global biota during the Ordovician Radiation was accompanied by a geographic and environmental expansion of genus ranges. The proportion of genera occurring in two or more paleocontinents in the database, and two or more environmental zones within a six-zone onshore-offshore framework, increased significantly in the Caradocian and Ashgillian. Moreover, widespread genera tended to be significantly older than their endemic counterparts, suggesting a direct link between their ages and their environmental and geographic extents. Expansion in association with aging was corroborated further by demonstrating this pattern directly among genera that ranged from the Tremadocian through the Ashgillian. Taken together, these results are significant not only for what they reveal about the kinetics of a major, global-scale diversification, but also for what they suggest about the interpretation of relationships between diversity trends at the  $\alpha$  (within-community) and  $\beta$  (between-community) levels.

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### Introduction

Despite previous suggestions that the geographic ranges of species may be direct consequences of their geological longevities (e.g., Willis 1922), it is likely that the extent of geographic or environmental coverage exhibited by a species results from the interplay of any number of environmental, ecological, and evolutionary factors. This is not to deny the possibility that species-aging might be associated, even intimately, with changes in geographic or environmental range, but, rather, to say that any such relationship could be eclipsed by other causal agents. Perhaps for this reason, the relationship that Willis proposed has been dismissed as a “quaint anachronism” (Brown 1995; p. 102). However, if we assume that any species must originate *somewhere*, a subsequent expansion outward from its point of origin seems inevitable (Yule 1924), suggesting that, at some scale, there must be a direct, if easily overshadowed, relationship of the kind that Willis suggested.

In an analysis of Late Cretaceous molluscs of North America, Jablonski (1987) found that the

geographic ranges of species were, indeed, significantly correlated with their geologic durations, but that geographic ranges were established early in the histories of individual species. Thus, in this instance, it appears that longevity was at least partly a consequence of geographic range, rather than the other way around. A relationship between geographic range and species longevity has also been suggested in several other studies on Cretaceous and Cenozoic molluscs (e.g., Jackson 1974; Hansen 1978, 1980; Jablonski 1980; Hoffman and Szubzda-Studencka 1982). While the species evaluated in all these studies may have initially undergone range increases that produced the relationship suggested by Willis, any such expansions must have taken place so rapidly that they would have appeared all but instantaneous in the fossil record.

Nevertheless, even if patterns exhibited by Cretaceous and younger molluscan species reflect those among the broader pool of marine invertebrates throughout the Phanerozoic, it does not necessarily follow that a relationship of the kind proposed by Willis could not be recognized at higher taxonomic levels. Because the

number of species constituting any higher taxon might change significantly through its geologic lifetime, it is possible that concomitant changes in geographic or environmental ranges could result, even if the individual ranges of constituent species appear to remain static. In this vein, Yule (1924) demonstrated quantitatively that, in a biota that is diversifying at both the genus and species levels, the species richness of a genus should, on average, increase significantly as the genus ages. If, as Willis (1922) showed, genera that are more species-rich also tend to be more widespread than their species-poor counterparts (e.g., see the table on p. 114 of Willis 1922), it follows that an aging genus should also become more widespread in concert with increasing species richness. Moreover, studies documenting "onshore-offshore" and other spatio-temporal patterns of diversification for Phanerozoic higher taxa (e.g., Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Bottjer and Jablonski 1988; Miller 1988, 1989; Jablonski and Bottjer 1990a,b) illustrate an association between diversification and environmental expansion; as a clade "ages," the area that it occupies may well change on a temporal scale that permits detection in the fossil record.

The Ordovician Radiation was a dynamic interval marked by substantial growth in global taxonomic richness (Sepkoski 1993, 1995, 1997; Miller and Foote 1996) and major shifts in the taxonomic, ecological, and morphological components of diversity (Sepkoski 1981; Bambach 1983, 1985; Foote 1993, 1994, 1995; Wagner 1995; Droser et al. 1996). It can also be shown that, at the genus level, the global biota aged significantly during the Ordovician Period (see below). In this paper, I demonstrate that there was a relationship between this transition and a contemporaneous expansion of the geographic and environmental ranges of genera. Moreover, the environmental range expansion of genera explains a possible discordance among Ordovician diversification patterns at the  $\alpha$  ("within-community") and  $\beta$  ("between-community") levels that might otherwise have been viewed as surprising, on the basis of previous empirical and theoretical treatments of Paleozoic diversification (e.g., Sepkoski 1988).

### Global Age-Frequency Distributions

The analyses presented below focus on a pool of genera (referred-to herein as *the study group*) that, combined, constituted a balanced cross-section of major contributors to each of Sepkoski's (1981) three Phanerozoic evolutionary faunas: trilobites; inarticulate and articulate brachiopods; monoplacophorans, gastropods, and bivalves. As demonstrated previously (Miller and Mao 1995; Miller and Foote 1996; Miller 1997), this aggregate group serves as a satisfactory proxy for the evaluation of synoptic diversity patterns exhibited by the broader set of taxa extant during the Ordovician.

Global age-frequency distributions of the study group from epoch to epoch through the Ordovician, based on data from Sepkoski's unpublished compendium of fossil marine genera, are presented in Figure 1A. The age of each genus that was extant during a given epoch was calibrated as the number of epochs since it first originated. There are broad tails on the age-frequency distributions for each epoch, reflecting the long-term persistence of a few genera that originated during the Cambrian. On the other end of the spectrum, the plurality of genera throughout the Ordovician was relatively young, reflecting the limitation of many genera to just a single epoch. However, the age-frequency distributions clearly illustrate the increasing richness of older genera as the Ordovician progressed; comparisons of the distributions of adjacent epochs using the Kolmogorov-Smirnov two-sample test ( $\alpha = 0.05$ ) indicate a significant epoch-to-epoch change in every instance starting with the Arenigian-to-Llanvirnian transition. In fact, in contrast to earlier epochs, the majority of genera in the Caradocian and Ashgillian were extant for two or more epochs.

Because the Ordovician Radiation was characterized by a broad transition from taxa with relatively high turnover rates, including trilobites, to others with lower turnover rates, including articulate brachiopods, bivalves, and gastropods (Sepkoski 1981, 1984; Gilinsky 1994), it might be argued that the apparent aging of the biota was a direct consequence of this transition: a biota dominated by taxa with lower turnover rates might, on average, be expect-

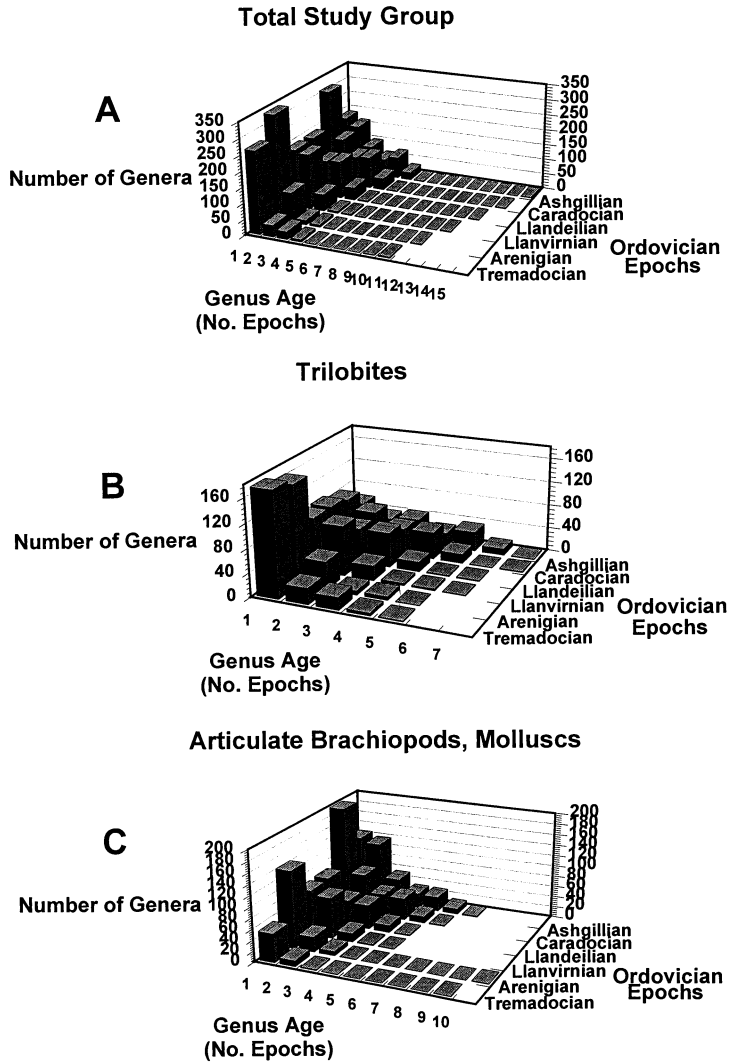


FIGURE 1. Comparison of the age distributions of Ordovician genera for the higher taxa in the study group, from epoch to epoch, based on data from Sepkoski's unpublished compendium of fossil marine genera. A, All genera in the study group; B, Trilobite genera; C, Articulate brachiopod, bivalve, gastropod, and monoplacophoron genera. The age of a genus during a given epoch was calibrated as the number of epochs for which it had been extant. Although the plurality of genera within each series tended to be relatively young, the age distribution of genera changed significantly through the period in that the number of older genera increased through the period, relative to the number of younger genera. The patterns depicted in B and C do not combine to produce the precise pattern illustrated in A because A also includes inarticulate brachiopods, a few of which were among the oldest Upper Ordovician genera in these data.

ed to contain a higher percentage of older taxa than one dominated by taxa with higher turnover rates. However, this possibility is dispelled here by considering the age distributions of trilobites separately from those of articulate brachiopods and molluscs (Fig. 1B,C). Clearly, trilobite and articulate brachiopod/mollusc subsets of the study group were both aging through the Ordovician, demonstrating

that the pattern exhibited by the entire study group was not an artifact of taxonomic transitions that characterized the Ordovician.

#### Assessments of Geographic and Environmental Ranges

*Geographic Ranges.*—For the analyses described below, I used a literature-derived database of some 6600 occurrences of 974 genera

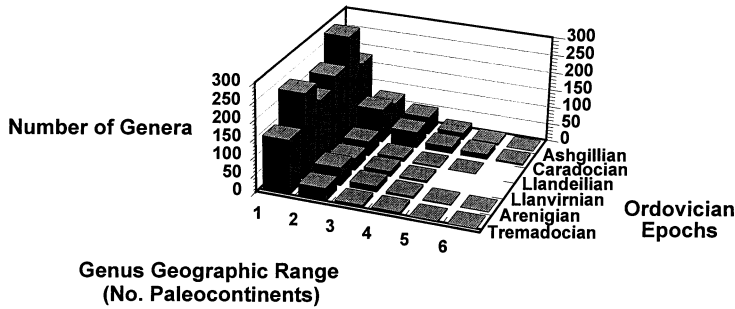


FIGURE 2. An epoch-to-epoch comparison of the paleogeographic ranges of genera in the study group, based on the database of Ordovician genus occurrences. Throughout the Ordovician, the plurality of genera were restricted to just a single paleocontinent, but the number of genera with broader geographic ranges increased significantly during the Caradocian and Ashgillian.

belonging to the study group, from Ordovician strata around the world (following the terminology of Miller and Foote 1996, an individual occurrence of a genus in the rock record is referred to as a *genus occurrence*). These data have been utilized previously in a series of investigations into the kinetics and selectivity of the Ordovician Radiation (Miller and Mao 1995, 1997; Miller and Foote 1996; Miller 1997) and were collected from published literature sources for several Ordovician paleocontinents: Laurentia, Avalonia, Bohemia, Baltoscandia, North China, South China, and, to a limited degree, Australia. Although the database does not yet include several other paleocontinents with appreciable Ordovician fossil biotas, it is already of sufficient extent to evaluate global-scale questions of diversity (see Miller and Mao 1995; Miller and Foote 1996).

Because the database depicts multiple occurrences of individual genera, it might be possible to determine directly for a given epoch the geographic ranges of genera, at least among the paleocontinents in the database, by mapping and measuring the paleogeographic extents of their occurrences limited to that epoch. However, because of continued uncertainty about the positions of several paleocontinents during the early Paleozoic (e.g., Dalla Salda et al. 1992a,b; Dalziel 1995; Thomas and Astini 1996), a definitive measurement of this kind is not currently feasible. For present purposes, the geographic range of each genus within each epoch was calibrated simply as the number of paleocontinents in which it oc-

curred during the epoch in question: endemic genera were limited to just a single paleocontinent, whereas more widespread genera were found in as many as six paleocontinents.

Geographic ranges of genera in the study group, from epoch to epoch through the Ordovician, are summarized in Figure 2. Throughout the Ordovician, the plurality of genera in the database were endemic. However, in the Caradocian and Ashgillian, the number of genera that occupied two or more paleocontinents increased significantly (confirmed with epoch-to-epoch comparisons of geographic range distributions using the Kolmogorov-Smirnov two-sample test at  $\alpha = 0.05$ ).

To evaluate this pattern further, the age distributions of Caradocian and Ashgillian genera with paleogeographic ranges of 1, 2, or  $\geq 3$  paleocontinents were compared with one another (Fig. 3). For this purpose, the ages of genera were determined directly from their stratigraphic ranges in the database, recognizing that, in a few instances, ages would be artificially truncated because (a) a small proportion of genera probably ranged back to the Cambrian, and the database does not include Cambrian occurrences; and (b) the database is not yet entirely worldwide in scope, and the initial appearance of any genus might be extended with data from additional paleocontinents. However, neither of these limitations is likely to have biased the patterns recognized in Figure 3, which show, for both the Caradocian and Ashgillian, that widespread genera tended to be significantly older than their

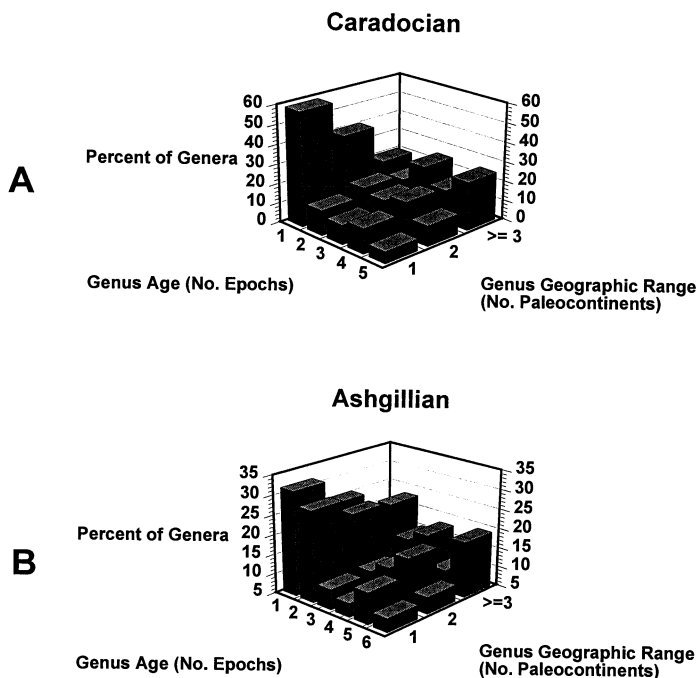


FIGURE 3. Comparisons of the age distributions of genera present in 1, 2, or  $\geq 3$  paleocontinents during the Caradocian (A) and Ashgillian (B) epochs. In both epochs, the ages of genera that were widespread, particularly those with geographic ranges of three or more paleocontinents, were older than their endemic counterparts, as evidenced by the increased percentage of older, relative to younger, genera.

endemic counterparts. For both epochs, genera with paleogeographic ranges of three or more paleocontinents had age distributions that were significantly different from those limited to a single paleocontinent (based on Kolmogorov-Smirnov two-sample tests, at  $\alpha = 0.05$ , on the raw values for each age class, rather than the proportional values illustrated in Fig. 3). Taken together, the patterns illustrated in Figures 1–3 suggest not only that the global biota was aging and that genera, on average, were becoming more widespread geographically, but that there was a linkage between these two transitions.

In addition, the age distributions exhibited in Figure 3 preclude any suggestion of an alternative scenario: that Ordovician genera established their geographic ranges early in their lifetimes, maintained these ranges throughout their stratigraphic/temporal extents, and were longer-lived in instances where they were more widespread. Such a pattern would parallel that exhibited at the species level as documented by Jablonski (1987) and others. However, if this had been

the case among Ordovician genera, then younger genera should have been represented on the roster of widespread Caradocian and Ashgillian genera in proportion to their overall representation during these two epochs. For example, the proportion of widespread Ashgillian genera that originated during the Caradocian should have been considerably larger than the proportion of widespread Ashgillian genera ranging back to the Tremadocian, given that the overall number of Ashgillian genera that originated in the Caradocian was more than six times the number that originated in the Tremadocian (162 versus 25; see Fig. 1). However, as illustrated in Figure 3, these proportions were nearly equitable (23.1 versus 19.2 among Ashgillian genera present in three or more paleocontinents), demonstrating that Caradocian genera were underrepresented among widespread Ashgillian genera, relative to what would be expected if geographic ranges of genera were established rapidly and then maintained throughout their observed stratigraphic/temporal ranges.

The suggestion that genera had a propen-

TABLE 1. Epoch-by-epoch averages of the number of paleocontinents and paleoenvironmental zones occupied by the suite of widespread Ashgillian genera that had persisted since the Tremadocian Epoch. For the paleocontinental calculations, genera were classified as widespread if they occurred in at least three paleocontinents during the Ashgillian ( $n = 15$ ). Similarly, for the paleoenvironmental calculations, genera were classified as widespread if they occurred in at least three Ashgillian environmental zones ( $n = 14$ ).

Epoch	Average no. paleocontinents	Average no. environmental zones
Tremadocian	1.6	1.6
Arenigian	1.8	2.2
Llanvirnian	2.6	2.8
Llandeilian	2.6	2.3
Caradocian	3.6	4.5
Ashgillian	3.9	3.7

sity to become more widespread geographically as they aged can be further confirmed empirically by focusing directly on geographic patterns exhibited through the Ordovician by a suite of relatively old genera that were particularly widespread during the Ashgillian. Among the Ashgillian genera in these analyses, 15 were found in three or more Ashgillian paleocontinents and ranged back to the Tremadocian. Based on their occurrences in the database, the average number of paleocontinents occupied by these genera was determined for each Ordovician Epoch (Table 1). This average increased regularly from epoch to epoch through the period, demonstrating that, as they aged, the geographic ranges of these genera increased.

Because the total number of genera was larger for the Caradocian than for other Ordovician series in concert with its longer duration (see Miller and Foote 1996), it might be argued that the apparent Llandeilian-to-Caradocian increase in the number of nonendemic genera is tied artifactually to an increase in the number of genera. However, this assertion can be countered in three ways:

1. The statistical significance of the difference between the Caradocian and earlier epochs, based on the Kolmogorov-Smirnov test as described earlier, suggests that the increase in the number of genera with ranges exceeding one paleocontinent is greater than that expected simply as a consequence of differences in the aggregate number of genera.

2. The enrichment in nonendemic genera is

maintained in the Ashgillian, even though there are far fewer Ashgillian genera in the database than there are Caradocian genera, concomitant with the shorter duration of the Ashgillian (see Miller and Foote 1996).

3. If the pattern were simply reflecting an increase in the number of genera, there would be no reason to expect that widespread genera in the Caradocian would also be older, on average, than endemic genera.

Given that there is some epoch-to-epoch variation in the relative proportions of data from different paleocontinents (e.g., South China has a disproportionately rich Arenigian fossil record [see Miller 1997]), there might be some concern that Late Ordovician increases in genus geographic ranges resulted from increases in the equitability of coverage for different paleocontinents in the database (i.e., proportionally speaking, a larger number of paleocontinents may have been more readily "available" in Upper Ordovician data). To evaluate this possibility, Shannon-Wiener Information Indices were calculated for each epoch, based on the proportions of genus occurrences in the database from each of the six principal paleocontinents. Relatively large values of the Shannon-Wiener index would reflect relatively equitable distributions of genus occurrences among the six paleocontinents. If the Shannon-Wiener index had increased regularly from epoch to epoch, concern might have been warranted that changes in equitability of occurrences among continents were affecting the observed geographic range patterns. However, the results (Table 2) demonstrate that equitability was rather comparable in most epochs; the calculated value for the Arenigian was noticeably lower than for other epochs because of the unusually large number of occurrences for South China. In any case, there is no indication that equitability increased in the Caradocian or Ashgillian, dispelling any suggestion that the geographic patterns described herein resulted from such an increase.

Finally, while the positions of several Ordovician paleocontinents continue to be debated (see Introduction), it does appear that some of the paleocontinents included in the database were converging as the Ordovician

TABLE 2. Epoch-by-epoch determinations of the Shannon-Wiener Information Index based on the proportional representation of genus occurrences in each epoch among the six principal paleocontinents and among the six paleoenvironmental zones.

Epoch	Paleocontinents	Paleoenvironmental zones
Tremadocian	0.70	0.71
Arenigian	0.57	0.70
Llanvirnian	0.76	0.67
Llandeilian	0.75	0.67
Caradocian	0.74	0.66
Ashgillian	0.73	0.72

progressed, in concert with the closing of the Iapetus Ocean (e.g., Laurentia, Avalonia, and Baltoscandia) (see Scotese and McKerrow 1990). This convergence might suggest that the apparent propensity of genera to occur in an increasing number of paleocontinents as the period progressed was a consequence of the growing proximity of some of these paleocontinents, rather than a true expansion of the geographic ranges of genera. However, the relationship between genus age and extent of geographic coverage provides compelling evidence that paleocontinental convergence is not responsible for the patterns recognized here. If convergence had produced the observed increase in the number of genera shared among paleocontinents, there would be no reason to expect that widespread genera would be significantly older than those limited to a single paleocontinent; young genera should have occurred on multiple paleocontinents just as commonly as older genera.

*“Environmental” Ranges.*—To investigate possible changes in paleoenvironmental ranges of genera during the Ordovician Radiation, a series of analyses were conducted paralleling those described above for the evaluation of geographic ranges. To conduct this part of the investigation, most genus occurrences in the database were assigned to one of six environmental zones arrayed from nearshore to deep water, using the protocol established in earlier research by Sepkoski and others (Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; Sepkoski 1988; Miller 1988); a small number of occurrences (fewer than five percent) could not be assigned definitively to an environmental zone and were excluded from these

analyses. Determinations of paleoenvironmental ranges were then based on occurrences of genera among the six environmental zones through the Ordovician. Clearly, measurement of the “true” environmental range of any taxon would likely encompass a far more complex, multidimensional treatment than just a simple assessment within a one dimensional, onshore-offshore framework. Nevertheless, it is probably safe to say that there is a positive correlation between the range of genus as measured here and its true environmental range.

An epoch-by-epoch summary of the environmental ranges of genera is shown in Figure 4; the pattern is similar to the depiction of geographic ranges in Figure 2. Most notably, Caradocian and Ashgillian patterns differ significantly from those of earlier epochs (Kolmogorov-Smirnov two-sample test at  $\alpha = 0.05$ ), reflecting a noticeable increase in the number of genera with environmental ranges of two more zones. As was the case with geographic ranges, environmentally widespread genera in both the Caradocian and Ashgillian had significantly different age distributions than genera restricted to a single environmental zone (Kolmogorov-Smirnov two-sample test at  $\alpha = 0.05$  on the raw numbers); on average, widespread genera were older than their more restricted counterparts. Moreover, epoch-by-epoch determinations of the average environmental ranges of the 14 genera that had persisted since the Tremadocian and were present in at least three Ashgillian environmental zones show a substantial increase in the Caradocian and Ashgillian (Table 1).

Thus, during the Ordovician Radiation, genera became more widespread environmentally as they aged. The possibility of an artifactual link to an increase in the equability of genus occurrences among environmental zones was again dispelled by calculating Shannon-Wiener Information Indices for each epoch, this time based on the proportions of genus occurrences from each of the six environmental zones (Table 2). As with the geographic data, there is little variation in these values and no indication of a trend of increasing equability through the period; in fact, the Caradocian exhibited the smallest value and

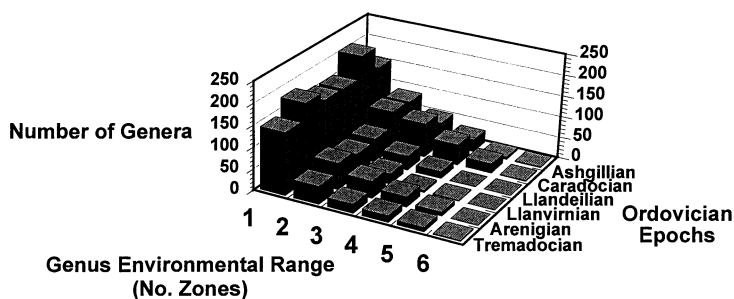


FIGURE 4. An epoch-to-epoch comparison of the paleoenvironmental ranges of genera in the study group, based on the database of Ordovician genus occurrences. Genus occurrences were assigned individually to one of six paleoenvironmental zones, arrayed in an onshore-offshore framework. Throughout the Ordovician, the plurality of genera were restricted to just a single paleoenvironmental zone, but the number of genera with broader paleoenvironmental ranges increased significantly during the Caradocian and Ashgillian.

the Ashgillian the greatest, even though both epochs were characterized by greater preponderances of widespread genera than earlier epochs.

### Discussion

As noted earlier, many Ordovician genera were ephemeral, in that they were restricted to a single epoch. However, as the period progressed, there was a growing pool of temporally persistent genera that became more widespread, geographically and environmentally, as an apparent consequence of their persistence. There are two plausible, end-member species-level scenarios that would produce such a pattern in a given genus: (a) the number of constituent species within the genus increases, and, thus, the aggregate range of the genus increases because the ranges of constituent species are not identical to one another; or (b) the constituent species richness of the genus does not increase but, rather, the actual ranges of species increase during their lifetimes at rates sufficiently protracted to be detected in the fossil record. Species-level data are not at hand to distinguish between these two possibilities for the Ordovician. Jablonski's (1987) Late Cretaceous research, described earlier, suggests that the first scenario might be more plausible than the second, but it is not clear that patterns among Late Cretaceous molluscs can be extrapolated to the Ordovician. Moreover, the analyses of Yule (1924; described earlier), coupled with investigations of clade dynamics using branching models (Raup 1985; Patzkowsky 1995a), dem-

onstrate the strong plausibility of the first scenario, but, they do not preclude the possibility of the second scenario.

Regardless of the species-level dynamics that produced the geographic and environmental expansions of Ordovician genera, the documentation of these patterns has significant ramifications for the reconciliation of diversity trends at different hierarchical levels. In a comparative analysis of local and global diversification, Sepkoski (1988) found a positive correlation between  $\alpha$  (within-community) and  $\beta$  (between-community) genus diversity trends during the Paleozoic Era: both  $\alpha$  and  $\beta$  diversity increased from the Cambrian to the Ordovician and then leveled-off, suggesting that they were directly related to one another. Sepkoski provided a theoretical scenario for this pattern, involving *contraction* of the environmental ranges of individual taxa in a world of increasing diversity (see Sepkoski 1988: Fig. 6).

However, in his empirical comparison of Paleozoic periods, Sepkoski (1988) presented data at the period level of resolution. Thus, it is possible that much of the increase in genus-level  $\beta$  diversity that Sepkoski recognized from the Cambrian to the Ordovician was concentrated in the earliest part of the Ordovician Period, and that a more highly resolved analysis might not have shown a persistent signal of increasing  $\beta$  diversity through the Ordovician Radiation. Indeed, in an analysis of North American articulate brachiopod assemblages, Patzkowsky (1995a) found no evidence of a parallel relationship between  $\alpha$  and



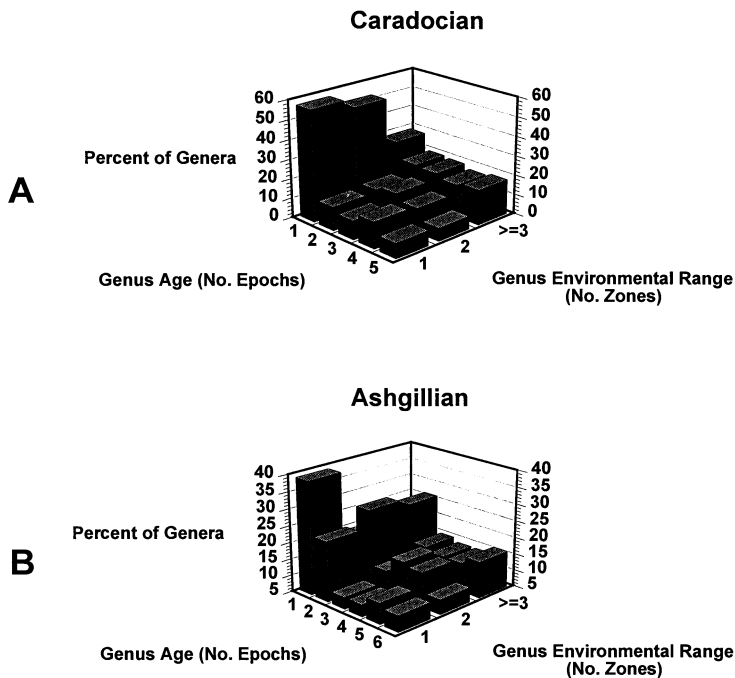


FIGURE 5. Comparisons of the age distributions of genera present in 1, 2, or  $\geq 3$  paleoenvironmental zones during the Caradocian (A) and Ashgillian (B) epochs. In both epochs, the ages of genera that were widespread, particularly those with paleoenvironmental ranges of three or more zones, were older than their more restricted counterparts, as evidenced by the increased percentages of older, relative to younger, genera.

$\beta$  diversity trends at the genus level. Whereas  $\alpha$  diversity showed a net increase through the period,  $\beta$  diversity wandered up and down with no net tendency. Moreover, primarily on the basis of analyses of data from South China, Miller and Mao (1997) suggested that  $\beta$  diversity may have actually decreased through the Ordovician, in contrast to  $\alpha$  and global diversity.

The environmental expansion of genera documented herein, which runs counter to the theoretical scenario described by Sepkoski (1988), would have served to decrease, rather than increase,  $\beta$  diversity, because it would have increased the similarity of assemblages from different environments to one another, even in the face of increased  $\alpha$  and global diversity.

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